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ANIMAL EVOLUTION

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There are few lines of scientific speculation of such general interest as the problem of the evolution of the varied assemblage of types included in the animal kingom, while at the same time a logical and detached consideration of this problem is rendered exceedingly difficult both because of the isolated position occupied by many of these types and by the conviction we all have that man must represent the highest of them.

But while undoubtedly man is the most efficient and the dominant member of the animal kingdom it by no means necessarily follows that he and his fellow vertebrates are from the strictly biological standpoint the most perfect.

In the following pages I shall indicate, as briefly as possible, a line of reasoning whereby all the various animal types are brought into correlation with each other, and their evolution is shown to be not evolution in the sense of a progressive development from a lower type to a higher, but instead the gradual acquisition of increasing economic efficiency through the progressively greater and greater departure from biological perfection, correlated with the gradual loosening of the bonds by which the most perfect type is economically handicapped.

In a very large and important group of animals, the Protozoa, the body is composed of a single cell; but in all animals except the Protozoa the body is composed of a very large number of cells which are differentiated to serve definite purposes.

All multicellular animals begin life as a single cell. As at this stage they are in this respect comparable in structure to a protozoan, in later life they may be assumed to represent an advance over the protozoan type.

The original cell giving rise to a multicellular animal typically divides into two, four, and eight similar cells, the cleavage taking place in three planes each at right angles to the other two; each of these eight similar cells continues to divide until a hollow ball is formed of numerous cells all of which are alike. Such a structure is represented by a blastula, but no adult animal (? except *Salinella*) which can be regarded as the equivalent of such a stage is known.

The hollow sphere with its increasingly thin walls due to repeated cell divisions becomes mechanically unstable and collapses, forming a cup with a two layered wall, the inner lining being composed of the inturned cells of the collapsed portion.

There is now a differentiation of the cells into an external and an internal layer, but each of the cells in both layers is the equivalent of all the others in the same layer. A definite axis has appeared, passing through the center of the mouth of the cup (the gastrula opening) and through the opposite pole.

Since in every plane passing through the central axis the body wall is just the same as it is in every other plane the continued development of such a typical gastrula would result in the formation of a radially symmetrical animal developed about the axis of the gastrula as a center.

The logical conclusion is that those animals which develop radially about the original axis are biologically the most perfect of all animals since they continue without interruption into the adult stage the original developmental plan.

There are two groups of animals which develop in this way. In one of these, the sponges, the larva grows into a sort of radial mass colony or imperfectly integrated community of cells with little division of labor or unified life and no definite organs. In the other, the cœlenterates, the gastrula grows into an adult which resembles it in all its essential features, though innumerable minor refinements are added.

The sponges, being without any definite structures, indeed little more than proliferated masses of slightly differentiated cells, increase in size by simply growing out in all directions from the main axis and usually also upward.

The cœlenterates retain the definite body form of the original gastrula which with increase in size rapidly weakens mechanically in spite of the development of a series of internal buttresses; furthermore, they have definite organs, such as tentacles, which must be supported by the body wall, and they must be strong enough to capture and to hold the organisms which serve them as food. They are therefore limited to a definite and relatively small body size, excepting in a few cases of extreme specialization. But just as in the sponges there is no definite limit to the original growth impetus. In response to this the original polyp, having reached its full size, gives off a bud which grows into another polyp and this process may be continued indefinitely so that enormous arborescent or other colonies are formed.

Both the sponges and the cœlenterates continue in the same way to increase in bulk throughout life, the former by simple augmentation of the mass as a whole, the latter by the indefinite reduplication of the original unit. The colonial habit is a fundamental attribute of all cœlenterates,

though many of them have secondarily become solitary through the disintegration of the colony coupled with an increase in size of the individuals.

Among the cœlenterates the solitary habit is commonly derived from the colonial through the process of strobilization. The original polyp elongates and from it plate-like units (ephyræ) one by one separate off by transverse fission distally which develop into large free living adults.

The original polyp which gives rise to the strobila is always at first bilaterally symmetrical, with two tentacles opposite each other. In the simpler cœlenterates the gastrula becomes the mouth of the adult, but in the more specialized types a considerable part of the external surface about this opening is drawn into it during growth forming a gullet tube.

Bearing these two facts in mind it is easy to reconstruct the path by which the so-called higher animals were evolved from the cœlenterate type.

Strobilization in the form characteristic of the cœlenterates became modified by the retention of the original bilateral symmetry and its accentuation, coupled with a more or less vague differentiation into a dorsal and a ventral surface, and the retardation of the liberation of the units formed, which are not detached until after sexual maturity has been reached, and furthermore have to a considerable degree lost their individuality, sharing a common nervous and excretory system. This condition is represented by the tape-worms, at the present time occurring only as parasites.

The next step was the further reduction in the individuality of the segments and their retention throughout life, resulting in the formation of a definite elongate jointed body composed of a series of similar segments in which a dorsal and a ventral surface are clearly distinguishable. Such a condition is represented by the annelids.

The unified body thus formed by the consolidation of what were originally separate and distinct entities in an animal colony which have now quite lost their individuality and become mere segments was still further perfected by the grouping of these segments into three units, the head, most unified, controlling and directing, the thorax, less completely unified, locomotor, and the abdomen, largest and least unified, containing the vital organs, as seen in the insects, or by a marked tendency to compress the body within the compass of a single group of firmly consolidated units, as seen in the crustaceans. In both cases the consolidation of the body was accompanied by a marked increase in the differentiation of the dorsal and ventral surfaces, and an extension of the former at the expense of the latter.

The body of the insects and crustaceans was thus derived from the colonial cœlenterates (as represented by the strobila) through the cestode and annelid types by the reduction of the colonial units to segments with progressively decreasing individuality accompanied by the modification of the

radial symmetry first to a symmetry in which the body is the same on either side of two planes at right angles to each other (as in the polyp giving rise to the strobila), then to a similar but much more pronounced symmetry of the same kind with a faintly indicated dorsal and ventral surface (as in the cestodes), later to a bilateral symmetry with well differentiated dorsal and ventral surfaces, the former usually somewhat more extensive than the latter (as in the annelids), and finally to a very pronounced bilateral symmetry with the dorsal surface always greatly in excess of the ventral (as in the crustaceans and insects). The two tentacles of the polyp from which the strobila develops persisted as the lateral extensions of the proglottides in the tape-worms (which sometimes reach a considerable length), and these reappeared as the parapodia of the annelids, and in their most perfected form as the legs and other segmental appendages of the arthropods.

Strobilization comparable to the type characteristic of the cœlenterates also occurs in another form. The units, instead of budding off in a linear series, are formed on the walls of the interior of a closed polyp which finally disintegrates, liberating all the enclosed units as free living individuals. These have a symmetry which is apparently bilateral, but always shows marked radial features. Such a development is found in the liver fluke and its allies, though today in no non-parasitic forms.

This method of growth by which young are actually seen to be budded off from the interior of a closed sack developed from the ciliated larva, combined with the more or less extensive infolding within the gastrula mouth of part of the outer body wall as seen in the more specialized cœlenterates, furnishes a clue to the origin of the unsegmented animals.

In those colonial cœlenterates with division of labor the polyps are divided primarily into nutritive, reproductive, and "defensive," but the last are characterized by an abundance of cells containing an excretion and a coiled tubule, and some or other of them are constantly discharging the included liquid. They are probably fundamentally excretory and only secondarily adapted for defensive purposes.

It is easy to imagine that in the early stage of some cœlenterate type the infolding of the outer cell wall at the gastrula mouth was sufficient to bring within the inner cavity the region from which the new polyps are budded off, and to assume that there then were given off internally three buds, one of the nutritive (sack-like), one of the reproductive, and one of the excretory type, which developed into the perivisceral, the gonadial, and the nephridial cœlome.

The so-called cœlomate animals with unsegmented bodies, none of which, in sharp contrast to the segmented animals, have any true appendages, thus represent a colonial cœlenterate in which the colonial development has been transferred within the original unit; and the development of

this internal colony has reached its maximum in the cephalochordates and the vertebrates.

The correctness of the interpretation of the segmented animals as primarily consolidated colonies is indicated by the retention in all the included groups—the cestodes, annelids, crustaceans, echinoderms and insects—of some form of asexual reproduction, budding, budding and fission, fragmentation, polyembryony or parthenogenesis which, though greatly reduced in the more specialized types, especially in the insects, may be traced back to the budding and budding and fission characteristic of the cœlenterate colonies.

The correctness of the interpretation of the unsegmented animals (except those with gill apertures) as ingrown colonies is indicated in all the included groups—the priapulids, sipunculids, molluscs, nemerteans, phoronids, brachiopods, and chætognaths—by the entire absence of asexual reproduction of any kind, this having been rendered impossible through the transference of the colonial development to the interior.

For the sake of clearness no mention has been made of the fact that the annelids, crustaceans, echinoderms and insects, belonging to the segmented series, also possess cœlomic structures and are to a certain extent therefore doubly colonial. In the annelids the two structural remnants of the primitive colony are about equally balanced. In the crustaceans and insects the cœlomic structures have almost disappeared in favor of the development of the segmentation. In the echinoderms the body is reduced to five half segments while the cœlome is highly developed.

With the segmentation and the development of the cœlome considered as derived from a fundamentally colonial habit there is no fundamental body form nor structure in the bilateral animals which cannot be traced back to an origin in the colonial cœlenterates. The cestodes and the trematodes represent the transition forms in which we see the colonial habit and the radial symmetry of the cœlenterate type breaking down and passing into the solitary habit and bilateral symmetry of the "higher" animals in which little or no traces either of the primitive radial symmetry or of asexual reproduction remain.

These numerous forms, the annelids, crustaceans, echinoderms and insects on the one hand and the priapulids, sipunculids, molluscs, nemerteans, phoronids, brachiopods, chætognaths, enteropneusts and vertebrates on the other are so inextricably entangled in a network of lines connecting each more or less definitely or vaguely with all the others and even crossing the gap between the two groups that it is quite beside the mark to speak of evolution in connection with them. Each phylum represents a sort of crystallization center about which a greater or lesser number of forms all showing but little deviation from a fixed type are closely grouped within a definite but broad and general structural complex.

Some of these crystallization centers or foci lie close together, as the crustaceans and the insects, while others are quite isolated, like the nemerteans, phoronids, brachiopods, chætognaths and echinoderms. They are not now connected by any intermediate forms, and there is no evidence that they ever were. Each represents a stable and economically efficient, circumscribed and distinctive, combination of structural characters crystallized out of a wide range of possibilities resulting from the disintegration of the cœlenterate type which has, so to speak, gone into solution.

Evolution, in the sense of progressive specialization, has been conclusively demonstrated within many groups, but always within restricted sections of these groups. There is no evidence that the larger groups, or the broader divisions within these groups, succeeded each other in any such way. The appearance of all the major multicellular animal types was probably simultaneous or nearly so, the original progenitor giving rise continually to innumerable variations in form, symmetry and organization most of which proved economically impossible, but many of which, proving suitable to meet a certain range of conditions, formed centers about which the various phyla were developed.

Whereas the animals between the cœlenterates and the enteropneusts are commonly considered as representing progressive evolution, this is not so in fact. It is true that they represent increasing bodily efficiency, but this bodily efficiency results from progressive structural deficiencies which throw into relief the features upon which this bodily efficiency is based. All the essential features of the bilateral animals preëxist in some form or other in the cœlenterates, but they can only become effective economically through the partial or more or less complete inhibition of others which here hold them in check.

Unimportant as they seem to most morphologists the possession of gill apertures characterizes a most interesting group of diverse animal types, the pterobranchiates, balanoglossids, tunicates, cephalochordates and vertebrates. In all of these except the balanoglossids there is a sudden return to the fundamental colonial habit in a modified form, as if the appearance of gill apertures marked the beginning of the senescence of the animal line as a whole which from that point on recapitulated, or rather paralleled, its earlier stages. In the cephalochordates and vertebrates the internal colony or cœlome becomes enormously subdivided, recalling more or less closely the conditions in the annelids; on the other hand in the tunicates there is practically no cœlome, but the formation of colonies by budding, which are often highly complicated and with division of labor, reappears. In the pterobranchiates (*Rhabdopleura* and *Cephalodiscus*) the formation of colonies by asexual budding is developed to a high degree.

From the preceding discussion it would seem that the only way by

which the numerous and varied animal types can be made to fall into any evolutionary plan is to consider the radially symmetrical colonial cœlenterates as representing the highest degree of purely biological perfection, and all other animals (except the sponges which are their equivalent) as derived from them through the appearance of various defects which had the anomalous result of leading to increased bodily efficiency.

THE CORRELATION OF TIME UNITS AND CLIMATIC CHANGES IN PEAT DEPOSITS OF THE UNITED STATES AND EUROPE

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This paper is a continuation of a previous publication[4] which contained a discussion of the evidence in peat deposits of the United States regarding climatic changes since the last Ice age.

For purposes of comparison a brief account in tabular form is presented to show certain correlations between peat deposits in this country with those of the continent of Europe.

1. A correlation of American with European *glacial drift sheets* has been made by Leverett.[8] By considering with Leverett the early and late Wisconsin Glaciation contemporaneous with the Würm glaciation it is possible to correlate the corresponding minor glacial stages.

The three readvances of the ice sheet that produced the morainic systems of the late Wisconsin: the Valparaiso-Kalamazoo, Lake Border, and Port Huron may be regarded as corresponding to Penck and Brückner's[10] cycle of mountain glaciations of the Alps: the Bühl, Gschnitz, and Daun-stadia—and to those of the Scandinavian continental ice-fields: DeGeer's[7] Dani-, Goti-, and Fini-glacial stadia.

2. *The Stratigraphic Study of Peat Deposits* in the United States has furnished valuable data as to the botanical composition of types of peat and their economic value. It has been shown also that the material formed under wet conditions differs in botanical composition and texture from that formed during dry periods, and that the study of separate and distinct layers in deposits formed within the main morainic systems during the glacial retreat serves to throw much light on the character of the past climatic changes.

Evidence is now presented by means of the position of conspicuous layers of forest peat, fibrous sedge and reed peat, and colloidal peat, to show the equivalence of peat deposits which were formed in the respective morainal belts of the United States and Europe. The greater structural complexity, it will be noted, is confined to areas within the oldest of the morainic